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PASTURE STUDIES (XXIX). INVESTIGATIONS ON THE LIGNIN FRACTIONS OF PASTURE HERBAGE AND OF THE FECES OF RUMINANTS

I. THE LIGNIN FRACTION OF PASTURE HERBAGE[1]

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The importance of lignin in relation to the digestibility of pasture herbage often has been emphasized. For a number of years the Pasture Committee of Macdonald College has been conducting studies on the digestibility of pasture herbage (5, 6). These and other studies have shown that the usual methods of feedingstuffs analysis are not always satisfactory and it has been proposed that the determination of lignin and cellulose be substituted for the crude fibre determination (7). It has been stated that not only is lignin itself indigestible but also that it limits the digestibility of other nutrients (7, 19). However, different investigators have reported very different coefficients of digestibility for lignin from similar materials (9, 14, 2, 7). This is an indication that further work is necessary on methods of lignin determination before it can be used as a measure of the digestibility of a feed. Present methods of lignin determination are empirical and no unequivocal proof is available that the same material is isolated from forage as from feces. Correct interpretation of analytical results is therefore difficult. It appears that a study of the amount and nature of the lignin isolated by different methods of analysis would supply information that might aid in securing a more accurate picture of the metabolism of lignin. Accordingly the present investigation is divided into three parts (1) a study of the lignin of immature pasture herbage; (2) a study of the lignin isolated from feces of ruminants fed immature herbage; (3) a study of the products formed by the high pressure hydrogenation of forage and feces. This paper presents the results of the investigation of the first problem.

REVIEW OF LITERATURE

The structure of lignin is still unknown. Eastham *et al.* (8) have stated "the structural theories of Freudenberg and of Hibbert are still highly speculative in nature". It is by no means certain that there is only one lignin, for Freudenberg (10) has postulated that lignin may exist in wood in different degrees of condensation, varying from single units to complex aggregates. If this theory be true, lignin or its precursors might exist in young succulent tissue such as forage, in forms varying from the polyphenols to highly complex molecules. Wood lignin, which may be considered as typical of pure lignin, is nitrogen-free and usually contains over 12 per cent methoxyl (21).

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The ultraviolet absorption spectra of lignin and related compounds have been studied by a number of different investigators—Herzog and Hillmer (13); Hagglund and Klingsted (12); Stamm, Semb and Harris (20); Glading (11). These investigators have indicated that lignin is aromatic in nature, and also that it has a characteristic ultra-violet absorption spectrum, with an absorption maximum in the region of 2800 Å. This absorption band has been ascribed by Patterson and Hibbert (18) to freedom of the position meta to the side chain of the phenylpropane lignin building units, and it persists in spite of alteration of the lignin molecule by methylation, acetylation or treatment with phenol, glycol or thioglycolic acid (11). It is shown by lignin isolated in a wide variety of ways, e.g., by modifications of the H_2SO_4 method, by the Willstätter HCl method and by Freudenberg's cupra-ammonium method. It also has been demonstrated (20) that the presence of pentosans has no effect on the shape of the absorption curve nor on the extinction coefficients when the concentration of the lignin solution is corrected for pentosan impurity. The extinction coefficients were not greatly affected by the formation of lignin derivatives if a correction was made for the increase in molecular weight caused by their formation, unless the group added to the lignin molecule itself absorbed light in the region of 2800 Å (11).

It has been stated (17) that spectrographic methods are capable of identifying lignin in solution at a concentration of 2 mgm. per litre. Adams and Ledingham (1) used a spectroscopic method to estimate the amount of lignosulphonate in solution.

In the chlorinated products of the sulphuric acid lignin fractions, however, the 2800 Å maximum is not well defined in most cases, and is very poorly defined in the lignin fraction isolated from herbage. In spite of this lack of definition, it seemed that the absorption spectra of forage lignins might give some evidence of their purity if they were compared with the spectrum of wood lignin prepared and dissolved in the same manner.

In view of the uncertainty of the chemical nature of the lignin of young plants it seemed that useful information concerning the amount of lignin in forage could be secured only if the material isolated as lignin was carefully characterized. This was done by determining the content of nitrogen and methoxyl in the lignin fraction isolated and by measurements of the absorption spectra and the solubility of the chlorinated products in bisulphite solution.

MATERIALS

Materials were obtained from digestibility trials conducted at Macdonald College in 1942 and 1943 (Crampton and Jackson (6)). In the former year the forage samples were collected in early June, mid-July and mid-September. These periods were chosen since previous work (Crampton and Forshaw (5)) had indicated the mid-season herbage to be of lower digestibility than that of early or late seasonal growth. Timothy was the predominating species in the herbage throughout the season. In the 1942 season no attempt was made to estimate the percentage contribution of this species to the sward. At each of the three harvesting periods the forage was about 3-5 inches in height. In 1943 the herbage was cut at intervals

of about three weeks over the period June 1 to September 14. The latter season was abnormally wet and the forage remained succulent throughout the entire experimental period. A full description of the forage, including the species composition of the sward, is given by Crampton and Jackson (6).

PREPARATION OF MATERIAL AND METHODS OF ANALYSIS

The herbage samples collected in 1942 were dried at room temperature and ground to pass a 0.5 mm. sieve before analysis. Two procedures of lignin determination were employed, that of Manning and DeLong(16)—hereinafter referred to as the standard method—and that of Crampton and Maynard (7). In order to obtain consistent results by the latter method, it was found desirable to allow the lignin suspensions to settle for five minutes after boiling off the chloroform, and to filter rapidly. In 1943 the fresh herbage samples were extracted twice in a Waring Blender with an ether-water mixture, such treatment having been shown (McDougall and DeLong (15)) to permit the isolation of a less contaminated lignin fraction. This air-dried residue was treated subsequently as in the standard method.

The methoxyl and nitrogen contents of the lignin fractions isolated from each of the forage samples studied were determined, the object being to define, to some extent, the relative purity of these fractions. The methoxyl determinations were made by the method of Clark (3) using hydriodic acid prepared as he recommended (4). In the determination of nitrogen the lignin fractions were isolated in tared Gooch crucibles, dried at 105° C. and weighed, then digested by the Kjeldahl process using mercury as a catalyst. The solution was made up to 100 ml. and the nitrogen content of a suitable aliquot was determined using a micro-distillation apparatus. The methoxyl and nitrogen contents were corrected for the amount of ash in the lignin isolates.

Lignin fractions obtained from forage by both the standard and the Crampton-Maynard methods of isolation were examined spectrographically. These samples were chlorinated while in the freshly isolated, still moist, condition by placing the Gooch crucibles containing them in a desiccator, washing the air out of the latter by means of a current of chlorine prepared from $KMnO_4$ and HCl, closing the outlet from the desiccator and leaving the latter connected with the generator during the chlorination process. The time of contact of the moist lignin preparations with the gas varied from several hours to over-night, and three or four such chlorinations were required to effect the complete removal of the lignin from the lignin fractions isolated by the procedures employed. The chlorination products were separated from the residual material by washing with 2 per cent Na_2SO_3 solution. Chlorination and extraction were repeated until the leachate was colourless. The residue was then washed with water, dried at 105° C., weighed, ashed, and weighed again, the result being the amount of insoluble lignin fraction. Definite weights of feces and forage samples, 0.500 and 1.000 gm. for the standard and the Crampton-Maynard method respectively, were taken for isolation of the lignin fractions. From determinations previously made on the same samples the amounts of lignin fraction isolable by each of the two methods was known. Thus the weight of material soluble in 2 per cent Na_2SO_3 solution after chlorination was

determinable with a fair degree of accuracy. The sodium sulphite extracts were diluted with distilled water to a concentration suitable for spectrographic analysis.

A lignin fraction which would serve as a standard was prepared by the 72 per cent H_2SO_4 method from a sample of ground maple wood which had been extracted successively with ethanol-benzene (1 : 2) for 24 hours, 95 per cent ethanol for 24 hours, and hot water for 12 hours. A sulphite-soluble extract was prepared from the lignin fraction of wood meal in the manner already described for the forage and feces samples. It may be noted, at this point, that, while the lignin fraction obtained from maple wood dissolved readily and completely in 2 per cent Na_2SO_3 solution after a single chlorination, the fractions obtained from forage had to be chlorinated several times and extracted several times (as indicated above) before maximum solution had been attained.

The absorption data were determined using a large quartz spectrograph, Littrow mounting, with a 30° quartz prism, the spectral range from 2510 Å to 3450 Å being investigated. The photographic plates were of the Eastman No. 33 type, and the match points on these were determined visually. The extinction values of the match points were read directly from the settings of the rotating sector. Absorption curves were drawn plotting E as the ordinate against wave-length (in Å) as abscissa, the value of E at 2800 Å then being read from the graph. The values of the specific extinction coefficient (k) were calculated from the formula $T = e^{-cdk}$, when T = transmission, c = concentration and d = depth of solution. The values of k for wood lignin were found to be 38.9 and 39.3 for concentrations of sulphite-soluble material of 0.036 and 0.0068 gm./litre respectively; the average of these (39.1) is in fair agreement with that reported by Glading (11) for "native" lignin from maple wood, viz., 41.7. This "native" lignin preparation probably was a purer material than the lignin fraction obtained in the present investigation and hence might be expected to have a higher specific extinction coefficient. The k values for the forage and feces lignin fractions isolated by both the standard and the Crampton-Maynard procedures were calculated in the manner indicated above. On the assumption that the specific extinction of the sulphuric-acid lignin obtained from maple wood is typical of lignin preparations of high purity, the relative purity of the fractions obtained from forage may be estimated from the formula $\frac{\text{k of test solution}}{\text{k of lignin solution}} \times 100$. This formula, of course, is, valid only in the event that any non-lignin materials present have no absorption at 2800 Å, and have no effect on the absorption of lignin.

EXPERIMENTAL RESULTS AND DISCUSSION

The data on the amounts of lignin isolated from the 1942 forage samples and the percentages of methoxyl, nitrogen and ash found in these lignin fractions are summarized in Table 1. The percentages of ash are reported for the 1942 samples only. The analytical results reported here represent the averages of two or more determinations. The lignin, methoxyl and ash data are reported on the dry matter basis and have been corrected for their ash content.

TABLE 1.—NATURE OF LIGNIN ISOLATED FROM FORAGE MATERIAL

(Moisture-free, ash-free basis)

Cutting period	Method of isolation	Lignin	Methoxyl in lignin	Nitrogen in lignin	Ash in lignin
		%	%	%	%
1942					
1	Standard	6.10	5.50	2.77	12
2	Standard	6.84	4.10	3.83	8
3	Standard	5.77	2.82	5.31	6
1	Crampton-Maynard	11.14	3.37	5.38	17
2	Crampton-Maynard	8.20	3.62	3.94	18
3	Crampton-Maynard	11.10	2.19	4.42	12
1943					
2	Standard	8.83	4.93	5.47	—
3	Standard	8.23	4.07	5.58	—
4	Standard	7.78	3.17	6.64	—
5	Standard	7.81	3.01	7.06	—
6	Standard	6.41	3.00	7.80	—

Table 1 shows that the two methods isolate widely different quantities of material. The fact that the material separated by the Crampton-Maynard procedure in all instances contained less methoxyl and, with one exception, more nitrogen also, indicates that this fraction contains more non-lignin material than does that isolated by the standard method. The Crampton-Maynard procedure separates a greater amount of methoxyl from 100 gm. of dry matter in all instances, the difference for 1942 samples being 15, 4 and 50 per cent for the three harvests respectively. On the assumption that the only source of methoxyl in the lignin fractions isolated is lignin, these data suggest that, although impure, the Crampton-Maynard lignin fraction actually contains more of the lignin of the sample than does the fraction isolated by the standard method. Nevertheless, even on the basis of the assumption that the Crampton-Maynard fraction contains more lignin than does that obtained by the standard method, the former must contain considerable non-lignin material since it is larger than the latter by 82, 20 and 92 per cent.

It will be noted that in 1943 the percentage of lignin fraction in the forage decreased continuously throughout the season. This decrease may be related to weather conditions which, as had already been noted, were abnormally wet. The actual decrease in the lignin content of the forage probably was greater than the decrease in the amount of the lignin fraction isolated, since there was progressively greater contamination of the latter by nitrogenous substances. There was also a decrease in the methoxyl content of the lignin fractions isolated from forage samples 3 and 4 as compared to that of sample 2. There was, however, little change in the methoxyl content of the fractions obtained from samples 5 and 6 even though the nitrogen content of these fractions continued to increase. The increased nitrogen content of the lignin fraction from samples 3 and 4 may be accounted for by the increased proportion of clover in the sward. On the other hand, although sample 6 contained a lower percentage of clover than sample 4, the nitrogen content of the lignin fraction isolated from the former was greater

than that separated from the latter. There is, nevertheless, the suggestion that the presence in the sward of varying proportions of leguminous plants may influence the degree of contamination of the lignin fraction with nitrogenous compounds. This suggestion is supported by the fact that when the proportion of clover in the sward increased from 30 to 65 per cent the Crampton-Maynard lignin fraction doubled in amount, Crampton and Jackson (6). Since each cutting was made at approximately the same stage of growth as judged by height of forage and since there were no hot dry periods to promote rapid maturity, it appears that the species composition of the sward has a very marked effect on the quantity of lignin fraction isolated by the Crampton-Maynard procedure. Such observations as these indicate the desirability of conducting lignin studies on pure species of forage plants at least until such time as more definitive methods for the determination of lignin are available.

The data obtained for the percentage purity of the lignin fractions from the forage samples are presented in Table 2. The values for the relative purity of the sulphite solutions were obtained by the calculation described in the methods of analysis. The data on the relative purity of the lignin fractions were obtained by multiplying the percentage solubility of the lignin fraction by the relative percentage purity of the sulphite solution obtained from it. This procedure was adopted after it was observed that the specific extinction and the sulphite solubility of the lignin fractions bore an inverse relation to each other in the duplicate determinations (the tabulated values are averages).

There is a tendency for the inverse relationship of the specific extinction and the sulphite solubility to hold true for the various samples and hence for the relative purity to be fairly constant. For the 1943 samples the

Table 2.—Relative purity of lignin fractions isolated from pasture herbage as calculated from values for the specific extinction coefficient as 2800 Å and the solubility in sodium sulphite solution: values for lignin fractions similarly isolated from maple wood used as the standard of comparison

Cutting period	Specific extinction coefficient (2800 Å)	Solubility in sulphite solution	Relative purity of solution	Relative purity of lignin fraction
		%	%	%
1942				
1 (S)*	20.2	83	52	43
1 C & M**	21.3	78	54	42
2 (S)	16.3	81	42	34
2 C & M	22.4	78	57	44
3 (S)	26.5	65	67	44
1943				
2 (S)	26.0	82	67	55
3 (S)	25.0	71	64	45
4 (S)	23.5	66	60	40
5 (S)	21.0	73	54	39
6 (S)	26	65	67	44

* (S)—Standard method.
** C & M—Crampton-Maynard method.

variation in the species composition of the herbage may obscure this; the relative purity is lower when there is a greater percentage of clover in the sward. It will be noted that the relative purity of the 1943 lignin fractions is in general higher than that of those isolated from 1942 samples. This may be attributed to the removal of soluble material from the 1943 samples before drying them. Since the relative purity of the Crampton-Maynard lignin fractions is the same as that of similar fractions obtained by the standard procedure, and since the amount of the former is considerably greater than that of the latter, the suggestion previously made (on the basis of the absolute amounts of methoxyl in these fractions) that the Crampton-Maynard fractions contain more of the lignin of the sample than do those obtained by the standard method is supported by the spectrographic date. There are at least three possible explanations of this difference: (*a*) the treatment previous to the isolation of the lignin fraction by the standard method may remove lignin; (*b*) the pre-treatment employed in the Crampton-Maynard procedure may fail to remove nitrogenous substances (such as tryptophane and tyrosine) giving absorption at 2800 Å, and, (*c*) the formaldehyde used in the latter procedure may react with the samples to give products absorbing light at 2800 Å.

Two of the striking characteristics of the lignin fractions isolated from herbaceous plant tissues at growth stages of increasing maturity are the very low methoxyl content of the material isolated from very young and succulent tissues, and the marked increase in this constituent of the lignin fraction as the maturity of the tissues increases. These features are usually considered to be due to a combination of two factors—contamination of the lignin fractions isolated from immature tissues, and increasing content of methoxyl per unit of lignin with increasing maturation. Beyond a relatively early stage in cellular development, however, it is difficult to visualize a mechanism for the methoxylation of lignin. It therefore appears probable that the contamination factor may be the more important. The spectrographic data lend support to this suggestion by emphasizing the fact that the amount of non-lignin material in the fractions isolated from succulent pasture forage is large.

Typical absorption curves obtained for lignin isolated by the standard method from the 1942 samples are shown in Figure 1. Lignin isolated by the Crampton-Maynard method and by the standard method from the 1943 samples gave similar curves and hence these are not presented. The curve obtained from a sample of wood lignin is shown for comparison.

These curves were drawn by plotting $E\,\frac{1\%}{1\text{ cm.}}$ as the ordinate against wave length (in Å.) as the abscissa. The $E\,\frac{1\%}{1\text{ cm.}}$ values were calculated from the extinction and concentration of the solutions using the relationship $E\,\frac{1\%}{1\text{ cm.}} = \frac{E}{C}$, where C is the concentration of sulphite-soluble materials in gm./100 ml. The concentration of sulphite-soluble material was corrected for the non-lignin substances present on the assumption that the wood fraction consisted of lignin only and pure forage lignin would have the same absorption at 2800 Å. as wood lignin.

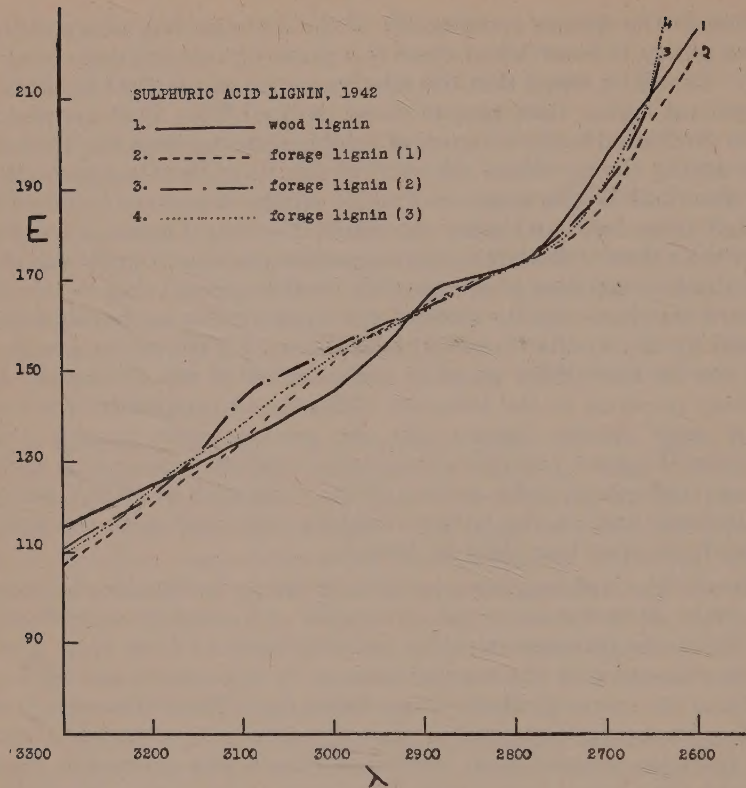

FIGURE 1. Absorption spectra of lignin solutions

The absorption curves for the forage lignin are generally similar to that obtained from wood lignin except that the break on the curve at about 2800 Å. shown by the latter is less pronounced or lacking in the former, but the similarity of the curves would indicate the presence of a material similar to wood lignin.

SUMMARY

The two methods of lignin determination that were studied were found to isolate widely different amounts of lignin from forage. The nitrogen and methoxyl values for the lignin fractions isolated indicated that these fractions differed also in their purity. It is possible that the Crampton-Maynard method isolated a less pure lignin than the standard method. It may recover more of the lignin of the sample, however.

Spectrographic data indicated that the lignin fractions isolated by either method were highly contaminated with non-lignin materials. The forage lignin contained large amounts of nitrogen and was low in methoxyl content (about one-third of the amount found in wood lignin).

It is also indicated that the ratio of clover to grasses in the immature herbage samples may influence the nature of the lignin fraction isolated.

In general the data here presented indicate that the current methods for determining lignin in young plant tissue are so inaccurate that conclusions respecting the digestibility of lignin based on the use of such analytical procedures are of questionable validity.

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PASTURE STUDIES (XXX). INVESTIGATIONS ON THE LIGNIN FRACTIONS OF PASTURE HERBAGE AND OF THE FECES OF RUMINANTS

II. THE LIGNIN FRACTION OF THE FECES OF RUMINANTS[1]

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In the preceding paper of this series (4) the authors discussed the problem of the determination of the lignin content of immature pasture herbage. Existing data on the digestibility of lignin were also discussed. The fact that the coefficients of digestibility of lignin have been found to vary widely suggests that lignin procedures isolate a variable entity which may not have the same composition when derived from feces as when derived from forage. Accordingly it was decided to study the nature of the lignin fraction of feces. It is the purpose of this paper to present the results of these studies. The pertinent literature has been reviewed in an earlier paper (4).

EXPERIMENTAL MATERIALS AND METHODS

Materials

The feces samples were obtained from the same digestibility trials as the forage samples (4). In 1942 a steer was used as the experimental animal while in 1943 the trials were conducted with sheep. In 1942 the feed was cut daily with a lawn mower and fed immediately and in 1943 the forage was cut at tri-weekly intervals and artificially dried. The feces samples were collected for the same sample periods as the forage samples (4).

Preparation of Material and Methods of Analysis

Composite feces samples were collected over a 4-5 day period. The aliquot obtained from each 24-hour feces collection was stirred with an equal volume of 95 per cent ethanol and filtered with suction. This procedure was adopted to facilitate drying of the feces sample. Drying in air was employed since it was thought that oven-drying might cause condensation of labile materials and result in a high yield of a very impure lignin fraction (2). The air-dried samples were combined to form the composite sample which was used for analysis. This sample was ground to pass a 0.5 mm. sieve.

In 1943 aliquots of the feces voided in each 24 hours were taken over a 10-day period and kept in a frozen condition to form a composite sample for analysis. Since it had been shown previously (3) that lower yields of lignin were obtained if the water-soluble material of forage was removed prior to drying, an attempt was made to evolve a method of removing as much of the nitrogenous and other interfering materials as possible from feces before drying for treatment with 72 per cent sulphuric acid. The method used for this purpose in the case of the forage material (extraction in the Waring Blendor with cold ether-water) was not satisfactory for feces since it was very difficult to dry the resulting residue. Extraction in the Blendor with a 10 per cent $CaCl_2$ solution was more rapid but three extrac-

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TABLE 1.—EFFECT OF METHODS OF PREPARING SAMPLES FOR 72 PER CENT H_2SO_4 TREATMENT

Treatment	Lignin in feces per cent	N in extracted material	N in isolated lignin	N of extracted feces in lignin*
		%	%	%
Oven dried				
Standard	15.66	2.49	4.27	76
1 per cent HCl, ethanol-benzene	16.32	2.19	3.82	73
10 per cent $CaCl_2$ ethanol-benzene, 1 per cent HCl	15.33	1.97	3.29	70
Frozen and extracted before drying				
Ether-water, ethanol-benzene, 1 per cent HCl	10.53	1.11	2.32	76
Ether-water, 1 per cent HCl ethanol-benzene	12.36	1.59	3.06	75
10 per cent $CaCl_2$, ethanol-benzene, 1 per cent HCl	11.72	1.14	2.49	77
Boiling water, 1 per cent HCl, ethanol-benzene	10.17	1.25	2.69	76

Note—Extraction treatments are listed in the order in which they were applied.

* Represents the percentage of the nitrogen of the extracted material that remains in the isolated lignin.

tions were required to remove the maximum amount of soluble material. The $CaCl_2$ solution was used in the hope that it would remove mucoproteins and thus facilitate drying. It was found that disintegration of the material in the Blendor followed by treatment with boiling water and 1 per cent HCl (both for 3 hours in the proportion of 150 ml./gm. dry wt.) gave as low a yield of apparent lignin as the ether-water extraction, though the lignin isolated after hot water extraction was somewhat more contaminated with nitrogen. As the hot water modification of the method was found to be the most convenient of those tried, it was used for the preparation of 1943 samples 2-6. The percentage of the nitrogen of the extracted materials remaining in the isolated lignin was calculated from data on the weights of the extracted material and of the lignin isolated from it and the nitrogen contents of these materials. The treatments and the resulting data are shown in Table 1; the extractions were carried out in the order indicated.

It is obvious that oven-drying results in the isolation of a larger amount of apparent lignin which is more contaminated with nitrogen than is the case with samples that are dried at room temperature, after removing soluble material. The methods of extracting the forage sample gave somewhat similar results though reversing the order of extraction with 1 per cent HCl and ethanol benzene gave a larger yield of the lignin fraction; this was also true in the case of the oven-dried sample. Extraction in the cold with ether-water or 10 per cent $CaCl_2$, drying, then extracting with ethanol-benzene yielded the lignin fraction least contaminated with nitrogen. Since 70-77 per cent of the nitrogen of the extracted material remained in the isolated lignin it is apparent that nitrogen must be removed prior to the 72 per cent H_2SO_4 treatment if a relatively pure lignin fraction is to be isolated.

The pre-treatment involving extraction with boiling water was most convenient to use, since the dissolved materials could be removed from the resulting suspension by filtration. In the case of extraction in the cold with ether-water, or with 10 per cent $CaCl_2$ solution, the resulting suspension had to be centrifuged. For this reason the boiling water-extraction of the feces materials was used for the samples collected in the 1943 season.

RESULTS AND DISCUSSIONS

Table 2 shows the percentage of lignin in the feces samples and the methoxyl, nitrogen and ash contents of the isolated lignin. These results represent the average of two or more determinations. The lignin values are reported on a dry matter basis and all figures have been corrected for the ash content of the crude lignin isolated.

The data indicate that the Crampton-Maynard method isolates a larger amount of lignin material than does the standard method; however, the Crampton-Maynard lignin probably is less pure since it is lower in methoxyl and higher in nitrogen in each instance. The Crampton-Maynard method does isolate a greater amount of methoxyl from 100 gm. of dry material in each case, the differences being 38, 21 and 36 per cent for samples 1, 2 and 3, respectively; the total apparent lignin isolated is, however, 80, 48 and 54 per cent greater. This indicates that the Crampton-Maynard procedure actually isolates more of the lignin of the sample although the product is less pure. This conclusion is further supported by the spectrographic data reported below. The fact that the lignin fraction isolated is more contaminated with nitrogen is an indication that pepsin digestion is less effective in the removal of nitrogen than is hydrolysis with 1 per cent HCl.

It is noteworthy that the lignin isolated from the 1943 samples is lower in nitrogen and higher in methoxyl than that isolated from the 1942 samples, in spite of the fact that the forage fed had a higher percentage of clover and hence was presumably higher in nitrogen in 1943. This may be due to the difference in pre-treatment procedure. It is also possible that the sheep digested interfering nitrogenous materials.

TABLE 2.—NATURE OF LIGNIN ISOLATED FROM FECES MATERIALS, RESULTS ON MOISTURE-FREE, ASH-FREE BASIS

Period	Method of isolation	Lignin	Methoxyl in lignin	Nitrogen in lignin	Ash in lignin
		%	%	%	%
1942					
1	Standard	14.85	4.84	3.47	25
2	Standard	16.18	5.09	4.19	16
3	Standard	16.32	3.63	4.14	17
1	Crampton-Maynard	26.69	3.74	4.49	33
2	Crampton-Maynard	23.92	4.59	4.74	28
3	Crampton-Maynard	25.08	3.23	4.68	23
1943					
2	Standard	14.75	6.60	3.67	—
3	Standard	15.57	5.96	3.61	—
4	Standard	12.39	6.10	3.31	—
5	Standard	11.65	5.38	3.63	—
6	Standard	8.74	5.34	3.21	—

It is interesting to compare the nature of the lignin isolated from feces with that of the lignin from corresponding forage samples as reported in the previous paper (4). Table 3 shows the average methoxyl and nitrogen contents of the lignin isolated from the 1942 samples of forage and feces by the standard and the Crampton-Maynard methods and from the 1943 samples by the standard method. The lignin isolated from forage is usually higher in nitrogen and lower in methoxyl than that recovered from feces. This indicates that the lignin fraction isolated from forage is less pure. If this estimate of purity is valid, then lignin digestibility coefficients calculated from such data would be too low. The methoxyl data are in contrast to those reported by Bondi and Meyer (1), who found feces lignin to be lower in methoxyl than forage lignin. The theory that lignin is demethoxylated in its passage through the animal body is not supported by our data.

TABLE3—METHOXYL AND NITROGEN CONTENTS OF FECES AND FORAGE LIGNINS

Period	Method of isolation	Methoxyl, per cent		Nitrogen, per cent	
		Feces lignin	Forage lignin	Feces lignin	Forage lignin
1942	Standard	4.51	4.14	3.93	3.97
1942	Crampton and Maynard	3.85	3.06	4.64	4.58
1943	Standard	5.88	3.64	3.49	6.51

TABLE 4.—RELATIVE PURITY OF LIGNIN FRACTIONS ISOLATED FROM FECES AS CALCULATED FROM VALUES FOR THE SPECIFIC EXTINCTION COEFFICIENT AT 2800 Å AND THE SOLUBILITY IN SODIUM SULPHITE SOLUTION; VALUES FOR LIGNIN FRACTIONS SIMILARLY ISOLATED FROM MAPLE WOOD USED AS THE STANDARD OF COMPARISON

Cutting period	Specific extinction coefficient (2800 Å)	Solubility in sulphite solution	Relative purity of solution	Relative purity of lignin fraction
		%	%	%
1942				
1 (S)*	23.8	67	61	41
1 C & M**	20.7	81	53	43
2 (S)	18.1	77	46	35
2 C & M	23.7	73	60	44
3 (S)	23.9	68	61	41
1943				
2 (S)	30.1	74	77	57
3 (S)	29.8	75	76	57
4 (S)	33.5	65	86	56
5 (S)	33.9	40	87	35
6 (S)	36.4	45	92	42

* (S)—Standard method.
** C & M—Crampton-Maynard method.

SPECTROGRAPHIC RESULTS

The spectrographic studies on the feces lignin were carried out in the same manner as those on the forage lignin.

The data obtained for the percentage purity of the lignin fractions isolated from the feces samples are given in Table 4. The values for the relative purity of the lignin solutions were calculated from the formula $\frac{\text{extinction of lignin test solution}}{\text{extinction of wood lignin solution}} \times 100$. The relative purity of the lignin fractions was calculated by multiplying the relative percentage purity of the lignin solution by its percentage solubility in sulphite.

It is noteworthy that, as judged by the spectrographic data, the Crampton-Maynard lignin fraction is as pure as the material isolated by the standard method. This may indicate that the former method actually isolates more of the lignin from the sample than does the latter. It is probable that although the fraction isolated is not completely soluble in sodium sulphite, all or most of the true lignin is removed, since there is an inverse relation between the extinction and sulphite solubility. Where the solubility in sulphite is low the extinction is high. The data indicate that the lignin isolated by either method is about 50 per cent pure.

Absorption curves were drawn, plotting $E \frac{1\%}{1 \text{ cm.}}$ as the ordinate against wave length (in Angstrom units) as the abscissa. The concentration of the sulphite-soluble material was corrected for non-lignin substance present on the assumption that feces lignin would show the same absorption characteristics as wood lignin. Absorption curves for lignin isolated from the 1942 samples by the standard method are shown in Figure 1. The absorption of a sample of wood lignin is shown for comparison. Lignin isolated from the 1943 samples and by the Crampton-Maynard method from the 1942 samples showed similar light absorption properties. The curves are similar to that of wood lignin and would therefore indicate the presence of a lignin-like material.

It has been shown in this and in the preceding paper that the lignin fractions isolated by current methods from either grass or feces may be highly contaminated by extraneous compounds, and may contain considerable percentages of nitrogen. The lignin isolated by the methods employed does not seem to be radically different in its chemical nature although certain pre-treatments may lower the content of nitrogen. However, the amount of apparent lignin may vary rather widely. It is therefore understandable that variations in reported digestibility coefficients are so great. It is obvious that a great deal of work remains to be done on the chemistry of the lignin of herbage and feces before any accurate picture of its metabolism can be obtained.

SUMMARY

The nature of lignin isolated by different methods from the feces of ruminants fed immature pasture herbage has been studied.

Both the pre-treatment and the method itself have great influence on the amount and nature of the fractions isolated as lignin. Spectrographic data indicated that these lignin fractions were about 50 per cent pure

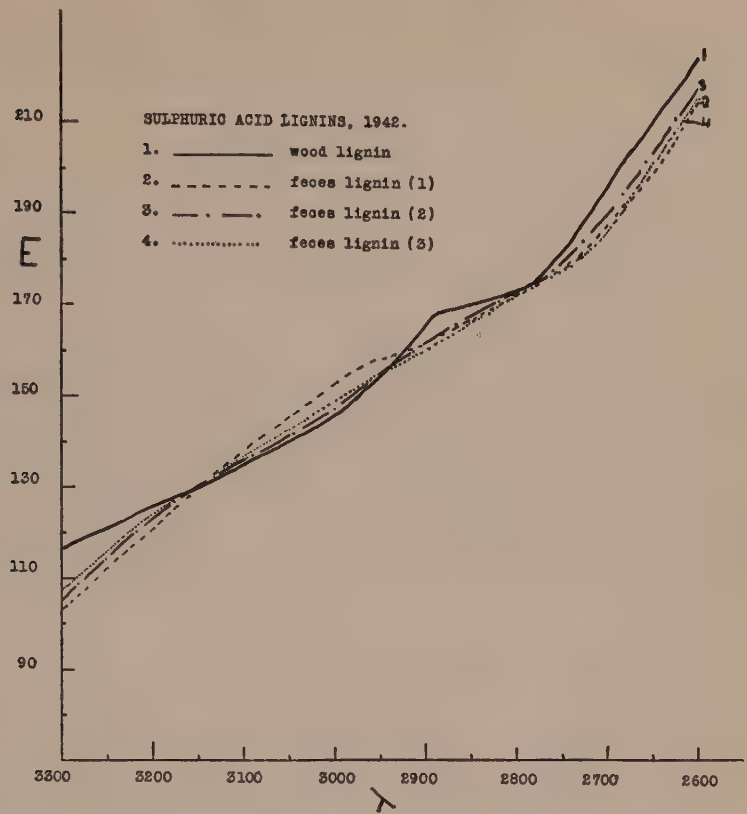

FIGURE 1. Absorption spectra of lignin solutions

relative to wood lignin. They contained relatively large amounts of nitrogenous material and were low in methoxyl. However, the data seemed to show that lignin was not demethoxylated in its passage through the animal body.

In view of the relatively low purity of the lignin fractions isolated by the methods studied, it is suggested that more intensive studies of the chemistry of grasses and of feces are required before the estimation of lignin will furnish an accurate index of the digestigility of herbage.

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SOME FACTORS AFFECTING APPLE YIELDS IN THE OKANAGAN VALLEY

VI. CONTENTS OF N, P AND K IN THE TERMINAL SHOOTS[1]

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In a previous paper in this series (25), the P, K and Ca contents of the soil were discussed. In this present paper the information obtained from analysis of the terminal shoots of apple trees is presented. Data obtained from leaf analyses will be presented in subsequent papers.

Prior to the start of this investigation (1937), terminal and twig analysis had been used to a considerable extent as a general measure of the quantities of certain nutrients absorbed by the roots. The results obtained by other workers gave encouragement to the hope by the author that the nutrient status of fruit trees could be readily determined by analysis of terminal shoots. At the present time, indications are that leaf analysis offers more promise than does shoot analysis. This investigation, however, has produced considerable information of value with regard to terminal shoots, their N, P and K contents, and the effects of certain factors on these contents.

REVIEW OF LITERATURE

Variation Within Shoot

In studies on the nutrient contents of the terminal shoots of fruit trees, considerable variation has been found in the concentrations of the nutrients from point to point within the shoot. In 1923, Harvey (9) reported finding decreasing amounts of N from the tip toward the base of the shoot. In 1931, Cullinan (4) obtained similar results. In 1935, Warne and Wallace (21) found a lower N content in the bark than in the wood of terminal shoots. Similar results were reported later by other writers (28). In 1936, Waltman (18) found that soluble N increased from the base to the tip of the shoot, but soluble P did not. In 1941, Davidson (5) recommended using the tip five-inch portions of apple shoots for analysis, rather than the whole shoots.

Seasonal Variations

In 1923, Harvey (9) found that in all parts of an apple shoot the N content, expressed in per cent of dry weight, decreased rapidly from June 2 to August 2, but showed little further change to September 11. In 1927, Thomas (13) reported that the per cent N decreased very rapidly in new shoots until full bloom, then less rapidly until fall, when it tended to increase again somewhat. Total N per shoot did not follow the same curve as did per cent N. Somewhat similar results were obtained in 1931 by Sullivan and Cullinan (12) with the apple and by Mulay (10) with the pear, and in 1941 by Williams (28) with the peach. In 1938, Vaidya (15) reported that in the bark of apple shoots, P decreased from June to September, then

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remained fairly constant until April. The K content, however, decreased from June to December. In the wood of shoots, both P and K decreased from June to September, rose slightly to December, then remained constant until April. In 1948, Beattie (1) found that shoot weight increased from June to September then held steady, while the N content of the shoots decreased rapidly till August then increased slightly. The total N per shoot, however, increased during the season. There appears to be general agreement that the N, P and K contents of the shoot tend to decrease rapidly early in the season, and to be at or near a minimum just prior to harvest.

Effects of Fertilizers

In 1927, Thomas (14) found increased amounts of N in apple shoots following application of nitrate of soda. Similar effects of N fertilizers have since been reported by a number of investigators (3, 11, 27, 28). In 1930, Davis (6) reported that when insufficient amounts of N and K were supplied to apple trees growing in pots, their contents in the shoots were reduced. Wallace (16) obtained similar results with P, K and Mg, and Waltman (19) with N and P. In 1933, Wallace and Proebsting (17) reported that K deficiencies were clearly reflected in the K contents of apple and plum shoots. In 1941, Davidson (5) recommended the use of analysis of extracts of green twigs for the purpose of determining nutrient deficiencies. There appears to have been general agreement that the higher the content of a nutrient element in the soil, the higher is its content in fruit tree shoots.

PROCEDURE

As reported in the first paper in this series (23), 400 mature McIntosh apple trees were selected in 1937 in grower-owned orchards in the Okanagan Valley. Most of these trees were selected in groups or "plots" of five, with one or more such plots in each orchard. Records of tree vigour, yield, and "profitable yield" were obtained over a six-year period (1937-1942) on 290 of these trees, in 73 plots (23). The "profitable" fruits included only those with more than 20 per cent of solid red colour and within the size range of $2\frac{1}{4}$ to $3\frac{1}{8}$ inches in diameter.

Each of the 73 groups or "plots" of trees was treated by the grower in accordance with his own orchard practices. For the most part, uniformity was maintained in the fertilizer and other cultural operations from year to year in any one plot. Sick trees, or trees on which the cultural operations were varied too much during the six-year period, were eliminated from the investigation.

Soil samples were obtained from each plot in the spring of 1940, at depths of 0 to 8, 8 to 24, and 24 to 60 inches. Where gravel and coarse sand mixtures were encountered above 60 inches, samples were not taken to the full depth. The procedures used and some of the results obtained have already been reported (24, 25).

Terminal shoot samples were taken in the fall of 1939 and again in the fall of 1940. The purpose of taking these samples for two years in succession was to cover both an "on" year and an "off" year with trees bearing biennially. The time of sampling was the last week of August and the

first week of September. As already noted in the "Review of Literature", this was the time when changes in nutrient content of the shoots had been found to be at or close to a minimum. Moreover, the N, P and K contents appeared to be at or close to minimum values just prior to harvest. As a check on results obtained by other workers, samples of shoots were selected periodically from six trees in 1938, four trees in 1939, and four trees in 1941. The data obtained from this will be presented below under "Results".

The procedure used in sampling the shoots was as follows: Select 10 terminal shoots growing outward and upward at an angle around the lower perimeter of the tree. Repeat this around the upper perimeter, to obtain a total of 20 shoots. Remove and discard the leaves, and cut off the tip 5 cm. portion of each shoot for analysis.

The main reason for selecting the tip 5 cm. portion only for analysis, rather than the full length of the current shoots, was to obtain a more constant proportion of meristematic tissue to total tissue. As already noted under "Review of Literature", highest percentages of N, P and K are found toward the tip of the shoot, in which part the proportion of meristematic tissue is also the highest. Where the shoots vary greatly in length, as occurred in this investigation, selection of the whole shoot causes a much wider variation in proportion of meristematic tissue to total tissue.

The shoot samples were allowed to air dry, and were then washed in hot 3 per cent H Cl to remove any adhering arsenical spray residues. They were dried to constant weight, weighed, and ground in a hand mill. Total N was determined (on only one or two trees in each plot) by a modification of the Kjeldahl-Gunning-Arnold procedure. For P and K analysis, an aliquot of dried material was wet oxidized with nitric acid and perchloric acid, by a modification of the procedure developed by Gerritz (7). Analyses for P and K were made as described in a previous paper in this series (25). Results were expressed in terms of parts per million of the dry weight of the shoot material.

Statistical analyses have been made of the data obtained, by methods already explained (23). Total yields were adjusted in turn for differences in size of tree, tree vigour, and biennial bearing, and profitable yields for differences in size of tree. These adjusted yields were then correlated with the two-year average N, P and K contents of the shoots. The biennial index (23) of each of N, P and K was calculated, and these in turn were correlated with one another and with the biennial indices for yield and terminal growth. Scatter diagram studies were made of each correlation.

RESULTS

Yields, tree vigour and other tree data have already been reported (23), as have also the soil analysis data (25). The records on shoot weights and N, P and K contents are so voluminous that no attempt will be made to present them in full in thispaper. It will be considered sufficient to note the seasonal trends, the coefficients of correlation, and the special fertilizer plot data.

Seasonal Trends

Changes that occurred in weight of the tip 5 cm. of shoots during 1938, 1939 and 1941 are illustrated in Figure 1. The weight increased until November in 1938 and October in 1939. Beattie (1) in New York reported that shoot weight of apples increased until September only.

Changes in the contents of N, P and K are shown in Figures 2, 3 and 4, respectively. It will be seen that in 1938 the N content dropped rapidly to July, then rose slightly to December. In 1939 and 1941, the P content

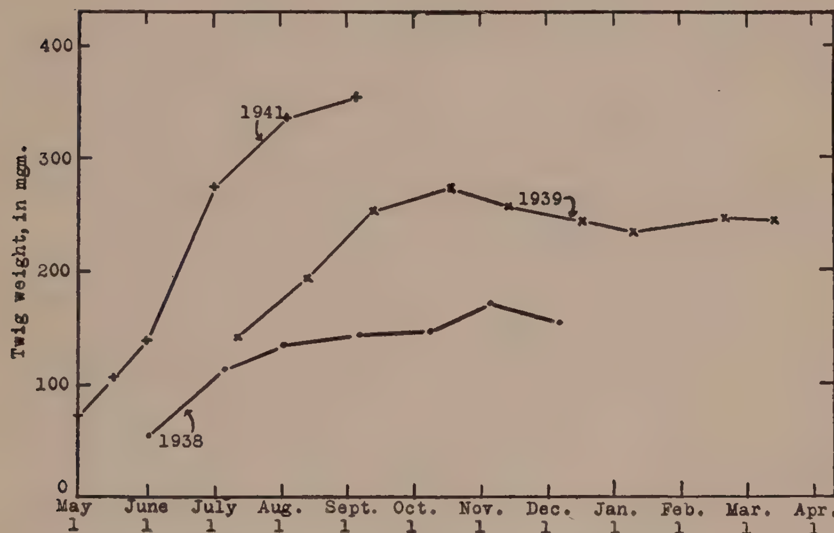

FIGURE 1. Trend of shoot weight during the growing season.

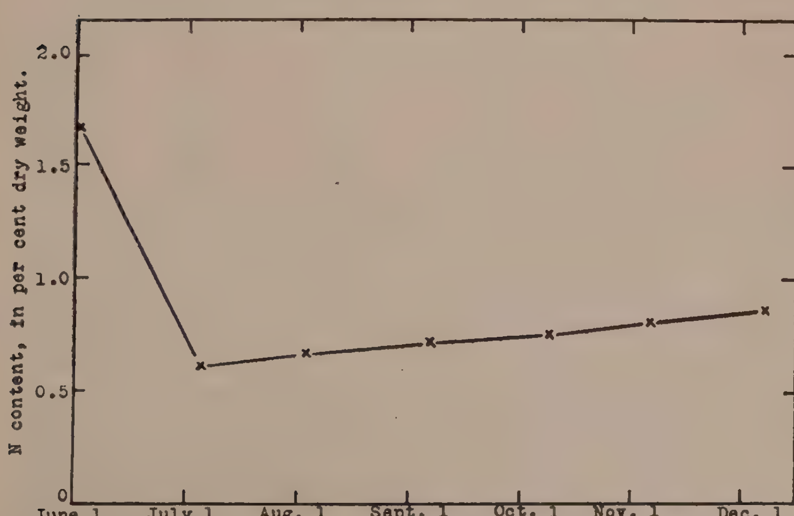

FIGURE 2. Trend of N content of shoots during the growing season.

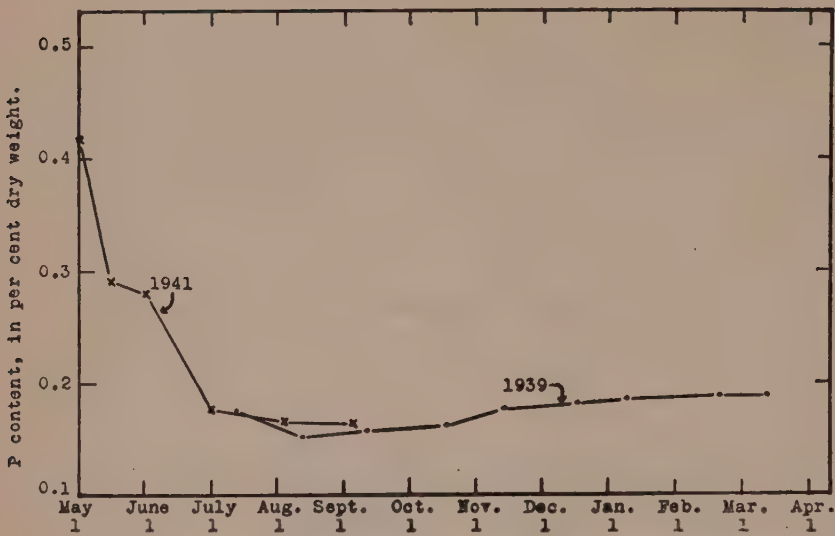

FIGURE 3. Trend of P content of shoots during the growing season.

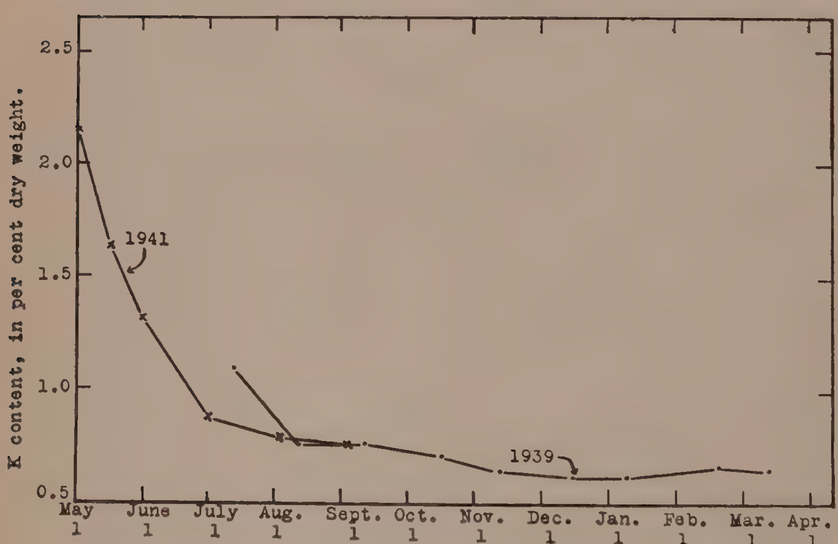

FIGURE 4. Trend of K content of shoots during the growing season.

dropped rapidly to July, less rapidly to August, then rose slightly to March while the K content dropped rapidly to July, more slowly to December, then rose again slightly over winter. In all cases, the most rapid changes occurred early in the season, while the shoots were still making their linear growth. The trend for N was similar to that reported by Thomas (13), and the P and K trends were similar to those reported by Vaidya (15). At the time of the main sampling—just prior to harvest—changes in N, P and K contents were slight.

Range of Values

The range of values obtained is important in the mechanics of both analysis and interpretation. Other things being equal, the greater the range in values the less difficulty arises from errors of chemical procedure, and the more readily can the data obtained be allocated to their class ranges. It is easier, for example, to divide the K content of a tissue into classes where it varies by several hundred per cent from sample to sample than where it varies by only 50 per cent or less.

The range of values obtained with N, P and K is summarized in Table 1. It will be seen that in all cases the extreme values obtained were not far apart; and this in spite of the fact that the trees sampled represented a very wide range in soil type and fertilizer treatment. This constitutes a distinct weakness in the use of shoot analysis as a means of diagnosing the nutrient status of fruit trees.

TABLE 1.—RANGES OF N, P AND K CONTENTS OF THE SHOOTS

Measurement	Year	Minimum	Maximum	Mean
N content, in per cent dry weight	1939 1940	0.503 0.587	0.988 1.076	0.712 0.818
P content, in per cent dry weight	1939 1940	0.132 0.136	0.211 0.203	0.170 0.166
K content, in per cent dry weight	1939 1940	0.550 0.500	0.830 0.820	0.692 0.642

Fertilizer Plots

Included in the 73 plots of McIntosh trees were three series of fertilizer plots. Yields and soils data from these plots have already been reported (26). In each series, the fertilizer treatments that had been applied over a period of years included a check plot receiving no fertilizer, a plot receiving nitrogenous fertilizer only, a plot receiving nitrogen plus phosphate, and a plot receiving nitrogen, phosphate and potash. The average shoot analyses of the trees in these plots are shown in Table 2. By way of comparison, there are also shown the P and K contents of the surface soil (26).

It will be noted from Table 2 that the N, P and K contents of the shoots showed little if any effect of fertilizer application. This is certainly not encouraging in so far as the use of shoots to diagnose the nutrient status of the trees is concerned. As noted in the "Review of Literature", other investigators have obtained excellent results in this regard, the content of an element in the shoots having been almost invariably increased by feeding this element to the roots.

An examination of the scatter diagram charts of the P and K contents of the shoots, from the whole 290 trees studied, indicates the possibility that the shoots reflect the nutrient status of the soil more accurately under conditions of nutrient deficiency than under conditions of nutrient sufficiency. In other words, differences in luxury consumption do not appear to be reflected accurately in shoots collected just prior to harvest.

TABLE 2.—FERTILIZER PLOT DATA

Element	Orchard	Year	Plot treatment			
			O	N	NP	NPK
N in shoots (%)	Barnard	1939	0.72*	0.91	0.90	0.92
		1940	0.81	0.94	0.79	0.75
	Baxter	1939	0.75	0.91	0.87	0.76
		1940	0.79	0.90	0.81	0.78
	Willis	1939	0.73	0.94	0.86	—
		1940	0.82	0.93	0.84	—
P in shoots (%)	Barnard	1939	0.17	0.17	0.17	0.17
		1940	0.17	0.15	0.18	0.18
	Baxter	1939	0.18	0.17	0.17	0.18
		1940	0.18	0.19	0.15	0.18
	Willis	1939	0.19	0.17	0.18	0.17
		1940	0.18	0.18	0.17	0.18
K in shoots (%)	Barnard	1939	0.77	0.72	0.75	0.78
		1940	0.90	0.84	0.71	0.79
	Baxter	1939	0.73	0.67	0.71	0.72
		1940	0.81	0.73	0.74	0.80
	Willis	1939	0.70	0.88	0.82	0.79
		1940	0.85	0.90	0.82	0.88
P in soil (p.p.m.)	Barnard	1940	2.8	3.3	11.6	10.2
	Baxter	1940	1.6	2.6	8.4	8.2
	Willis	1940	1.4	4.8	12.4	—
K in soil (p.p.m.)	Barnard	1940	93	105	91	132
	Baxter	1940	74	80	90	110
	Willis	1940	88	84	87	—

* Each figure for % N has been obtained from only one tree in the plot. Each figure for % P or K is an average of the values obtained from three or five trees in the plot. Each figure for p.p.m. P or K in the soil is from a composite 4-5 inch sample obtained from 10 locations in the plot.

As noted in a previous paper (16), no yield response from P or K has yet been obtained in these three series of fertilizer plots, indicating that there is as yet no proof of any deficiency of these elements in the three orchards represented. This, then, may explain the lack of response in the P or K content of the shoots.

It will be noted that application of phosphate has been accompanied by a marked increase in the available P content of the soil, but that application of potash has induced only a small increase in available K. These soils were already rich in available K without fertilizer treatment.

Effect of Biennial Bearing

Many of the 200 trees were addicted to biennial bearing, i.e., a heavy crop one year followed by a light crop or no crop the following year. The total yield per tree was used in determining the degree of biennial bearing. From the yields of each of two consecutive years was calculated the "biennial bearing index" of each tree as follows:

$$\text{Biennial bearing index} = \frac{100 \text{ (difference between two yields)}}{\text{sum of two yields}}$$

Complete annual bearing gave an index of zero, and complete biennial bearing an index of ± 100. When the yield of the second year was the

heavier, the index bore a plus sign; and when the yield of the first year was the heavier, it bore a minus sign. In computing averages over a period of years, these signs were ignored. This same procedure was used for calculating the biennial indices for terminal length, shoot weight, % N, % P, and % K in the shoots.

In order to determine the effects of biennial bearing on the shoot weight and its N, P and K contents, correlations were calculated among the biennial indices concerned. Those results of interest are presented in Table 3. An examination of the coefficients of correlation reveals that when a tree is bearing biennially, the following situation is found in the "on" year as compared with the "off" year:

Higher yield
Longer terminal shoots
Thinner terminal shoots (near the tips)
Higher N content of shoots
Lower P content of shoots
Lower K content of shoots

Recent work by the author (not yet reported) indicates similar effects of biennial bearing on the leaves as are reported here on the shoots.

The effects of biennial bearing on length and diameter of terminal shoots have already been discussed (22, 23). The lower P and K contents in the shoot and leaf tissues during the "on" year can be attributed primarily to heavier utilization of these elements by the developing fruits. Why the N content is higher in the "on" year is more difficult to explain. Wander (20) in Ohio has found more N in apple leaves during the "off" year, but Cain and Boynton (2) in New York have reported finding more N in the "on" year, and more P and K in the "off" year.

TABLE 3.—CORRELATIONS BETWEEN 1939-40 BIENNIAL INDICES

Two sets of data correlated		Coefficient of correlation
Biennial bearing index	Biennial terminal length index	+ 0.634**
Biennial bearing index	Biennial shoot weight index	− 0.625**
Biennial terminal length index	Biennial shoot weight index	− 0.561**
Biennial N index	Biennial bearing index	+ 0.330**
Biennial N index	Biennial terminal length index	+ 0.682**
Biennial N index	Biennial shoot weight index	− 0.225*
Biennial P index	Biennial bearing index	− 0.231**
Biennial P index	Biennial terminal length index	+ 0.023
Biennial P index	Biennial shoot weight index	+ 0.154*
Biennial K index	Biennial bearing index	− 0.316**
Biennial K index	Biennial terminal length index	− 0.379**
Biennial K index	Biennial shoot weight index	+ 0.459**
Biennial N index	Biennial P index	+ 0.601**
Biennial N index	Biennial K index	− 0.322**
Biennial P index	Biennial K index	+ 0.038

** Coefficient of correlation highly significant (odds greater than 99 : 1). * Coefficient significant (odds between 19 : 1 and 99 : 1). Coefficients not marked are considered non-significant (odds less than 19 : 1).

These results have an important bearing on the selection of plant material for evaluation of its nutrient status. The possibility of variations occurring in the nutrient content of fruit tree shoots or leaves, as a result of differences in cropping, indicates the advisability of selecting plant material from trees cropping to the same degree. The question arises as to whether sampling should be done on trees heavy in crop or light in crop. If it is considered desirable to determine each nutrient when it is present in least sufficiency, then the above data suggests the "off" year for N and the "on" year for P and K. The next best approach would appear to be to take composite samples representing an average degree of cropping in each case, and to set up standards of sufficiency on this basis.

Correlations with P and K Content of Soil

Correlations between the P and K contents of the shoots and the P and K contents of the soil are summarized in Table 4. Good positive correlations were obtained between the available P content of the soil and the P content of the shoots. This is rather surprising, in view of the apparent lack of such a relationship in the three series of fertilizer plots discussed above. The correlations between the available K content of the soil and the K content of the shoots were positive but non-significant. A possible explanation for this difference between P and K can be drawn from the assumption made above that the P or K content of the shoot bears a closer relationship to that in the soil when the supply of available P or K in the soil is low. On the whole, the soils in the 73 plots appear to average much lower in P content (relative to sufficiency) than in K content. It would be anticipated, therefore, that the coefficients of correlation between the P contents of the soil and the shoots would be greater than those between the K contents of the soil and the shoots.

Effects on Tree Vigour and Yield

To determine the relationships between N, P and K contents of the shoots on the one hand and the vigour and yield on the other hand, the data were averaged for two or more years and were then correlated. Only two years of records (1939 and 1940) were averaged with shoot weight and N, P and K contents, while four to six years of data were averaged with terminal length, biennial bearing index and yield. The correlations obtained are presented in Table 5.

TABLE 4.—CORRELATIONS BETWEEN P AND K CONTENTS OF SHOOTS AND SOIL

Two sets of data correlated		Coefficient of correlation
P in soil 0- 8 inches	P in shoots†	+0.289*
P in soil 8-60 inches	P in shoots	+0.311**
P in soil 0-60 inches	P in shoots	+0.319**
K in soil 0- 8 inches	K in shoots	+0.185
K in soil 8-60 inches	K in shoots	+0.041
K in soil 0-60 inches	K in shoots	+0.196

** Highly significant (odds greater than 99 : 1).
* Significant (odds between 19 : 1 and 99 : 1).
† Average of two years, 1939 and 1940.

The coefficients of correlation in Table 5 are disappointingly low in comparison with those in Table 3. Outstanding are the strong positive correlations between the N and P contents, between the P content and the shoot weight, and between the P content and terminal length. It appears that either N and P occur together naturally in these soils, or else they occur together in the shoots because of their close physiological relationship.

Of special interest also is the significant positive correlation between the N content and the length of terminal shoots. The question arises, then, as to whether average terminal length can safely be used as a measure of the N status of the tree. As noted elsewhere (26), the average terminal length of fruit trees is now being used in the Okanagan Valley as a basis for recommendations with respect to nitrogenous fertilizers. A more accurate procedure would undoubtedly be to determine the N content of the tree tissue. While one shoot analysis is being made, however, a large number of terminal lengths can be measured. So far, there has been little evidence in the Okanagan Valley of effects of soil nutrients other than N on tree vigour. The use of terminal length as a measure of N requirements would no doubt be less reliable in other areas, suffering from deficiencies of soil moisture or nutrients other than N.

Table 5.—Correlations between nutrient contents of shoots and tree performance

Two sets of data correlated		Coefficient of correlation
Average N content†	Average P content	+ 0.410**
Average N content	Average K content	− 0.039
Average P content	Average K content	− 0.037
Average N content	Average shoot weight	− 0.065
Average N content	Average terminal length	+ 0.280*
Average N content	Average biennial bearing index	− 0.098
Average N content	Total yield	+ 0.262*
Average N content	Profitable yield	+ 0.171
Average P content	Average shoot weight	+ 0.300**
Average P content	Average terminal length	+ 0.126*
Average P content	Average biennial bearing index	+ 0.098
Average P content	Total yield	+ 0.049
Average P content	Profitable yield	− 0.044
Average K content	Average shoot weight	+ 0.103
Average K content	Average terminal length	+ 0.165
Average K content	Average biennial bearing index	+ 0.149
Average K content	Total yield	− 0.129
Average K content	Profitable yield	− 0.152

** Highly significant (odds greater than 99 : 1).
* Significant (odds between 19 : 1 and 99 : 1).
† Averages of the two years, 1939 and 1940, were used with the shoot weight and the N, P and K contents. Six-year averages were used with terminal length, biennial bearing index and yield.

No significant relationship is revealed in Table 5 between the N, P or K content and the biennial bearing index. This was rather a surprise, as observation appears to indicate lessened biennial bearing with greater vigour. The fact that neither the N content of the shoots nor terminal

length has been correlated closely with the degree of biennial bearing can be attributed primarily to meteorological conditions (23). Among these conditions are late spring frosts and (to a lesser extent) winter killing of fruit buds. It appears also that growth conditions at time of fruit bud initiation are partly responsible.

With one exception, the correlations with yield (in Table 5) were not statistically significant. A significant positive correlation was obtained between the N content of the shoots and yield. This confirms the close relationship previously reported (23) between terminal length and yield. There were, however, very low correlations between P content and yield, and negative (non-significant) correlations between K content and yield. It appears from this that there have been no general deficiencies of P and K encountered in this investigation. If such deficiencies have occurred, they have been effectively masked by other factors. It is difficult to explain the negative correlations between K content of the shoots and yield.

DISCUSSION

The data presented in this paper give little encouragement for the use of shoot analysis as a means of determining the nutrient status of fruit trees. It is quite possible that the method could be used satisfactorily where marked deficiencies of certain elements occur; but it has not proved reliable in this investigation as a measure of the amounts of available P or K in soil containing more than the minimum requirements. From this viewpoint, both soil analysis and leaf analysis have proved more satisfactory. Whatever method is used, it should be one that provides ready measurement not only of deficiency of an element, but also of the degree of sufficiency.

Stress needs to be laid on the proper selection of tree tissue for analysis. It appears to be generally conceded (5, 8) that for routine analysis it is important always to select only one type of tissue, and to do so at only one part of the season. In addition to this, however, it appears desirable to collect samples only from trees showing a certain degree of cropping. To determine P and K deficiencies, sampling during the heavy crop year shows good promise. To determine the status of nutrients other than N, it also appears desirable to standardize the type of tree used, with regard to degree of vigour.

The use of shoot analysis has not revealed any deficiencies of P or K in the soils of the Okanagan Valley. The possibility that such deficiencies may actually exist has, however, been suggested by soil analysis (25). The final proof of deficiency of P or K is considered to be plant response to fertilizer application, and selected orchards showing low P and K contents of the soil are now being tested for such response by the field plot technique.

SUMMARY

Tree vigour and yield were recorded for six years on 290 mature McIntosh trees in the Okanagan Valley. Soil samples were taken at depths of 0-8, 8-24 and 24-60 inches. During two successive years, samples

of terminal shoots were collected prior to harvest, and the tip 5 cm. portions were analysed for total N, P and K contents. Shoot samples were also collected at different periods during the season.

During the growing season, shoot weight increased until after harvest; the N content dropped rapidly till July, then rose somewhat; the P content dropped rapidly till August, then rose slightly; and the K content dropped rapidly till July then more slowly till December.

The ranges of N, P and K values obtained were not large, in spite of wide variations in soil type and in fertilizer treatment.

The application of N, P or K fertilizer had little effect on the N, P or K contents of the shoots. Indications were that the N, P and K contents of the shoots reflect variations in the respective nutrients in the soil less accurately when they are present in sufficiency than when they are present in deficient amounts.

Biennial bearing of the trees was found to affect the N, P and K contents of the shoots in any one year. During the "on" year the terminal shoots grew longer but were narrower near the tips, the N content was higher, and the P and K contents were lower, then during the "off" year.

Correlations between the available P content of the soil and P in the shoots were positive and significant, and between the available K content of the soil and K in the shoots positive but non-significant.

Strong positive correlations were obtained between the N and P contents of the shoots, between the N content and terminal length, between the P content and terminal length, and between the P content and shoot weight. Correlations between the average N, P and K contents and the degree of biennial bearing were very low and non-significant.

Correlations between the N content of the shoots and the yield were positive and significant. Those between the P and K contents and the yield, however, were not statistically significant.

It is concluded that the use of shoot analysis has not revealed any deficiencies of P or K in Okanagan Valley apple orchards; also that shoot analysis does not show great promise as a means of diagnosing the nutrient status of fruit trees.

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THE PERFORMANCE OF SOUTHERN STRAINS OF BROME GRASS IN WESTERN CANADA[1]

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Brome grass is the most important cultivated forage grass in Western Canada. Following the period of extensive settlement of the Prairie Provinces after 1900 brome grass became widely used for hay and pasture purposes and frequently escaped from cultivation to form a common grass cover on road sides, abandoned lands, and other disturbed areas. In recent years a keen interest has developed in certain districts within the general adaptation area in the production of brome grass seed. Of a total Canadian production of 7,594,000 pounds in 1947 the Provinces of Manitoba, Saskatchewan, and Alberta produced 7,500,000 pounds[4]. The greater part of this seed has been exported to the United States.

In 1943, Newell and Keim (10) indicated that local Nebraska strains of brome grass which they termed "southern" strains were much superior to introduced or "northern" strains under conditions in Nebraska. The marked superiority of southern strains subsequently found in several adjoining states and the dependence of Canadian seed production on markets in the United States made it imperative to study the performance of southern strains in Western Canada. Since 1938, comparative trials of northern and southern brome grass strains have been conducted at eight Dominion Experimental Stations in Western Canada and at the Dominion Forage Crops Laboratory, Saskatoon, Sask. This paper summarizes forage and seed yield data from these tests and presents observations of plant type and growth behaviour made at the Dominion Forage Crops Laboratory, Saskatoon, Sask.

LITERATURE REVIEW

The occurrence of reasonably distinct types within the species *Bromus inermis* Leyss. which differ in morphology and adaptation was first pointed out by Zerebina (12, 13, 14). Zerebina made an extensive collection of native and cultivated brome grass strains within different districts of the U.S.S.R. and studied this material together with small collections from Western Europe, the United States, and Canada at the plant-breeding stations of Detskoe Selo (60° N. latitude) and Kammenaya Steppe (51° N. latitude). Two main ecological-geographical groups were recognized: (1) the "meadow" group or northern climatype, and (2) the "steppe" group or southern climatype. Descriptions of these two groups indicate correspondence with northern and southern types subsequently observed within the United States.

Zerebina observed that roots of the steppe group were distributed at a greater depth in the soil than the roots of the meadow group but there was no consistent difference in the extent of horizontal rhizome development

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[4] Production Reports. Plant Products Division, Production Service, Dominion Department of Agriculture. 1948.

between the two groups. Plants of the steppe group were slightly shorter and more erect than those of the meadow group. In the steppe group the main level of vegetative tillers was one-half that of the reproductive tillers whereas in the meadow group the main level of vegetative tillers approached two-thirds that of the reproductive tillers. Leaves of the steppe group were coarser in texture, shorter, narrower, and more erect than in the meadow group. They were also darker green in colour and bore more waxy bloom than leaves of the meadow group. Short narrow panicles were more commonly found within the steppe group, but no differences in seed characters could be found. Flowering was later and less prolonged in the steppe group. In regard to disease resistance the steppe group was found more susceptible to rust (*Puccinia bromina* Eriksson) and the meadow group more susceptible to brown spot (*Pyrenophora bromi* Died.).

Native collections showed the distribution area of the meadow type in the U.S.S.R. to extend from Murmansk in the north to the Caucasus in the south although south of the Central Chernozem Region this type was generally confined to valleys and more moist habitats. The steppe type accompanied the meadow type in the Central Chernozem Region and predominated in the dry steppe areas of the mid and lower Volga districts, Kazakstan, the northern Caucasus, the Eastern Ukraine and the southern Altai districts of Asia. Collections of cultivated brome grass from America and most of the collections of cultivated brome grass from within the U.S.S.R. were found to be of the northern or meadow type. Representatives of the true steppe type were rarely found in collections of cultivated brome grass but representatives of an intermediate type approaching that of the southern group were frequently found in cultivated collections from the Central Chernozem Regions, the central and lower Volga districts, and Western Siberia.

In America, Newell and Keim (10) studied a considerable number of brome grass strains obtained from northern and southern seed sources at Lincoln, Nebraska (40° N. latitude) and found strains from southern areas to be much higher in hay production than strains from northern areas. In the first year of production southern strains also yielded more seed but in the second year of production this situation was reversed with northern strains yielding more seed. Southern strains also had more vigorous seedlings which were better able to withstand heat and drought conditions. The more rapid growth of southern strains in the spring was considered an indication that these strains were earlier than northern strains. Additional evidence of the superior adaptation and forage productivity of the southern type in the States of Kansas, Iowa, Ohio, and Missouri has been given by Anderson (1, 2), Wilsie *et al.* (11), Lambert (9), and Brown (4). The varieties Achenbach, Fischer, Lincoln, and Elsberry are certified varieties of the southern type which have been developed within these states mainly from old established fields. In Michigan, Churchill (5) found the advantages of southern strains of brome grass to be less evident. Although these strains were more aggressive and higher in forage yield the lower protein content of the southern strains resulted in a lower total production of protein per acre than was obtained from northern strains.

Newell and Keim (10), Anderson (1), and Hansen (8) have reviewed the history of the introduction of brome grass to the United States. Southern strains were shown to arise from introductions from France and Hungary around 1880, while northern strains came from importations from Russia during the period 1896-1898. Introductions from Russia were on a large scale and extensively distributed with the result that brome grass of the northern type soon predominated in the American seed trade. In Canada, Fletcher (7) reported the introduction of brome grass from Germany about 1888 and the distribution of seed samples throughout all of Canada. It was the one grass above all others introduced to find uniformly good acclaim in Western Canada.

MATERIALS AND METHODS

Seed of the southern strains included in these tests was provided by the United States Department of Agriculture and the Agricultural Experiment Stations of states developing these strains. Seed of the northern commercial type was obtained locally at each station conducting a test, while seed of named and numbered strains of the northern type was obtained from the University of Saskatchewan, Saskatoon, Sask., and the Dominion Forage Crops Laboratory, Saskatoon, Sask.

Tests were conducted at the Dominion Experimental Stations at Beaverlodge, Lacombe, and Lethbridge in the Province of Alberta; at Swift Current, Melfort, Saskatoon, and Indian Head in the Province of Saskatchewan; and at Brandon and Morden in the Province of Manitoba. These stations represent a range in latitude from 49° N. latitude at Morden to 55° N. latitude at Beaverlodge. The stations at Lethbridge, Swift Current, and Saskatoon are within the drier brown and dark brown soil zones while the remaining stations are within the more moist black soil zone. The soil types represented by these stations vary from clays to clay loams.

The type of test employed, the varieties included, and the method of establishment varied from station to station. In general, however, randomized block designs were used and four or six replications provided. All tests were sown in the spring as is the general practice in this area and first yields taken in the second year of establishment. At all stations comparisons were made with brome grass growing as the pure species but at Indian Head, Saskatoon, and Brandon comparisons were also made with brome grass growing in combination with alfalfa.

Varieties have been designated as northern or southern in type according to the similarity of plant type and frost reaction to that of northern commercial brome grass or the Achenbach strain of the southern type. In certain cases stations originating strains were consulted as to type. The distinction of strains on the basis of frost reaction was considered quite critical as southern strains showed distinct superiority in the ability to remain green in the fall after the first light frosts had occurred and in the ability of overwintering stands to recommence growth in the spring.

RESULTS

Hay Production

Twelve tests of hay production of northern and southern types were carried out by the nine stations conducting tests. Although the first test was sown in 1938 most of the tests were carried out from 1944-1948. A summary of hay production in these tests is presented in Table 1 along with information on the nature of the tests and the latitude of the testing stations. In recording the results for each test varieties were grouped into the northern and southern types and the average yield of each brome grass strain for the full period of testing was expressed as a percentage of the yield of the northern commercial strain. Statistical analyses of results were not carried out for certain stations and due to the fact that different strains entered the various tests an analysis of combined results was not possible. It should be pointed out that in these tests strains were grown as the single species and that only one cutting per year was obtained except for the irrigated test at Lethbridge where two cuttings were obtained in two of the three years of testing.

No consistent advantage was shown for either the northern or southern type in production of forage although at certain stations the northern type was significantly higher in yield and at others the southern type was significantly higher in yield. As an average of the 11 tests in which both the northern commercial strain and the Achenbach variety were compared the yields of forage were almost equal. At Saskatoon, Lethbridge, Swift Current, Brandon, and Morden southern strains on the average yielded more than northern strains, while at Beaverlodge, Lacombe, and Indian Head northern strains on the average outyielded southern strains. It is difficult to explain the better performance of either type at certain stations in terms of latitudinal or climatic differences. In general the northern type yielded better at more northern stations and the southern type better at more southern stations. The low average yield of northern commercial in pounds of hay produced per acre shown in certain tests at Saskatoon, Swift Current, and Morden is indicative of the dry conditions under which tests were run at these stations. The relatively good performance of the southern type at these stations may be taken as an indication of greater drought resistance in this type. On the other hand at Lethbridge under irrigated conditions, where drought was not a factor, southern strains still outyielded northern strains.

At the Swift Current station much better persistence was found for the Achenbach strain than for the northern commercial strain or the Parkland variety. In a test sown in 1938 it was found by 1948 that stands of both northern strains had been thinned with a ingress of other species while stands of the Achenbach strain were complete in all replicates. This observation would also indicate superior adaptation of the southern type to regions of low rainfall and high summer temperatures.

In the irrigated test at Lethbridge where two cuttings were obtained in two of the three years of testing the production of hay of both types was rather similar in all cuttings. These results are in contrast to those of Newell and Keim (10) who found southern strains producing over twice as much as northern strains in early cuttings.

TABLE 1.—HAY YIELDS OF NORTHERN AND SOUTHERN BROME GRASS STRAINS AT NINE STATIONS IN WESTERN CANADA. HAY YIELDS EXPRESSED AS PERCENTAGES OF NORTHERN COMMERCIAL BROME GRASS

Strain	(1) Beaver-lodge	(2) Melfort	(3) Lacombe	(4) Saska-toon	(5) Saska-toon	(6) Saska-toon	(7) Indian Head	(8) Leth-bridge	(9) Swift Current	(10) Swift Current	(11) Brandon	(12) Morden	Average eleven tests
Northern Type													
Commercial	100	100	100	100	100	100	100	100	100	100	100	100	100
Parkland	—	98	100	97	—	96	89	—	96	104	98	117	—
Superior	—	193	—	—	94	100	—	—	—	98	—	—	—
S-23-7	—	101	—	—	—	—	89	—	—	91	—	—	—
S-23-12	—	—	107	—	—	—	95	95	—	—	85	103	—
Western Iowa	—	—	104	—	—	98	—	96	—	—	87	—	—
Iowa—1158	—	—	—	109	84	—	—	—	—	—	—	—	—
Average	100	100	103	102	93	98	93	97	98	98	92	107	—
Southern Type													
Achenbach	—	96	83	113	84	103	83	102	96	121	113	115	101
Lincoln	70	—	90	108	101	104	99	106	—	—	105	111	—
B. in. —9	95	—	85	116	—	119	93	107	—	—	107	121	—
Fischer	96	—	88	—	—	112	92	108	—	—	113	111	—
N.E. Nebraska	96	—	87	—	—	—	87	108	—	—	122	117	—
Iowa synthetic	80	—	—	—	—	—	—	—	—	—	111	—	—
Elsberry	—	—	—	—	98	—	—	—	—	—	—	—	—
Average	87	96	87	112	94	110	91	106	96	121	112	115	—
Level of significance:													
Strains	—	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	—	—	—	—	
Type	—	n.s.	1%	5%	n.s.	5%	n.s.	1%	—	—	—	—	
Yields of northern commercial tons per acre per cut	1.72	1.34	1.74	1.15	1.44	1.32	2.04	2.86	1.15	0.43	1.87	0.59	
Years of testing	2	4	3	4	3	2	3	3	4	3	3	3	
Replications	1	4	4	6	4	6	4	4	4	4	4	4	
Latitude of testing station degrees	55	53	52	52	52	52	51	50	50	50	50	49	

Within the group of northern strains no strain has shown any superiority over the commercial strain in general use. The Parkland and Superior varieties and strains S-23-7 and S-23-12 which were the result of selection for the reduced creeping habit are slightly lower in yield than the commercial type. The two strains of the northern type coming from Iowa also appeared similar to the northern commercial type in forage production. Within the group of southern strains no strain appeared to excel other strains of the group in forage yield.

Seed Production

Observations of seed production were made in conjunction with tests of hay production at Beaverlodge, Saskatoon, and Morden. In the test at Beaverlodge and the three tests at Saskatoon actual seed yields were obtained while at Morden seed yields were estimated on the basis of seed culm production. Yields of seed for these tests are summarized in Table 2. Strains have been grouped according to type and the production of each strain has been expressed as a percentage of the production of the northern commercial strain.

TABLE 2.—SEED YIELDS OF NORTHERN AND SOUTHERN STRAINS OF BROME GRASS AT THREE STATIONS IN WESTERN CANADA. SEED YIELDS EXPRESSED AS PERCENTAGES OF THE YIELD OF THE NORTHERN COMMERCIAL TYPE

Strain	(1) Beaver-lodge	(2) Saskatoon	(3) Saskatoon	(4) Saskatoon	(5) Morden	Average 4 tests
Northern Type						
Commercial	100	100	100	100	100	100
Parkland	—	29	—	59	100	—
Superior	—	—	95	122	—	—
S-23-12	—	—	—	—	96	—
West Iowa	—	—	—	110	—	—
Iowa-1158	—	74	92	—	—	—
Average	100	68	96	98	99	100
Southern Type						
Achenbach	—	49	57	49	47	51
Lincoln	56	28	41	64	61	44
B. in. —9	81	31	—	71	61	—
Fischer	56	—	—	82	53	—
N.E. Nebraska	91	—	—	—	53	—
Iowa synthetic	78	—	—	—	—	—
Elsberry	—	—	57	—	—	—
Average	72	36	52	66	55	48
L.S.D. strains per cent (P = 0.05)	—	35	24	38	—	—
Yield of northern commercial in lb. per acre	605	85	616	109	—	—
Years of testing	2	3	1	1	3	—
Replications	1	6	4	18	4	—

Marked differences were found in the seed production of northern and southern types in all tests. In no test has any strain of the southern type equalled the yield of the northern commercial type nor has any other strain

of the northern type significantly outyielded the northern commercial strain. On the basis of four tests the Achenbach variety yielded 51 per cent of the northern commercial type and the Lincoln strain 44 per cent of the northern commercial type. These results are in marked contrast to the results of Newell and Keim (10) who found that the seed yields of the southern type were significantly superior to the yields of the northern type at least in the first year of production. It was observed in tests at Saskatoon that seed yields from all strains were greatest in the first year of harvesting and the superiority of the northern types was most apparent in that year. Seed yields of the strain from western Iowa and strain 1158 from Iowa were comparatively high, thus indicating a preservation of the characters of the northern strains even though these strains were maintained for some time in southern areas. The Parkland variety generally recognized as a low seed producing strain showed very low seed production in two tests at Saskatoon.

Mixtures with Alfalfa

In view of the recognized advantages of growing northern brome grass in combination with alfalfa it was desirable to test strains of the southern type in mixtures with alfalfa also. The dense sod forming characteristic of the southern strains suggested that these strains might prove unusually competitive in combination with alfalfa thereby reducing the proportion of alfalfa in the mixture and the consequent advantages arising from the legume. Tests at Indian Head and Brandon were made of northern and southern strains in mixture with Grimm alfalfa. In these tests no advantage was shown for northern or southern strains in the mixture as far as total yields of the mixture were concerned. Unfortunately no separation analyses were carried out to show the proportion of legume in the mixture but general observation indicated no strain as being so aggressive as to eliminate alfalfa from the mixture. A test of mixtures was sown at Saskatoon in 1946, but the proportion of alfalfa in the mixture has remained small and the test has been essentially one of the grass alone. Separation analyses were made in this case and these showed all strains of brome grass of both southern and northern types to have similar amounts of alfalfa in the mixture except for the Parkland strain where the amount of alfalfa was significantly greater than for any other strain.

Morphological and Physiological Differences

Differences in leaf, stem, and panicle characteristics of northern and southern types as noted by Zerebina (12) were found to correspond reasonably well with differences between northern and southern types observed in these studies. Figures 1 and 2 show typical plants of the two types under conditions at Saskatoon. The most marked difference between plants of the two types was in the nature of the leaf. Leaves of the southern type were borne at a lower level on culms and were wider, coarser, and more glaucus than leaves of the northern type. Panicles of the southern type were more contracted and at maturity generally showed less anthocyanin development. Seed produced from northern and southern types in variety tests at Saskatoon was checked for bushel weight and weight per thousand seed and no differences found. Seed of the southern strains appeared more

FIGURE 1. Typical plant of the northern type.

FIGURE 2. Typical plant of the southern type.

chaffy, however, due to the more flaring lemma margins of seeds. A critical comparison of rhizome development in single plants in the second year of growth did not indicate a significant difference between northern commercial and the Achenbach variety in the extent of rhizome development. However, southern strains were observed to form a denser turf which was more difficult to plow up after the grass had been down several years. No difficulty has been experienced at Saskatoon in the eradication of either type.

The southern type at Saskatoon flowered two to four days later than the northern type and consequently may be considered slightly later at Canadian latitudes. Later flowering for the southern type was also observed by Zerebina (12) at somewhat comparable latitudes. Newell and Keim (10) and Lambert (9) considered northern strains later than southern strains on the basis of retarded development of the northern strains in the spring of the year. Under greenhouse conditions, Evans and Wilsie (6) and Atwood (3) found the northern type to be earlier than the southern type.

Two diseases causing leaf deterioration of brome grass at Saskatoon, particularly in years of high rainfall, are brown-spot caused by *Pyrenophora bromi* Died., and leaf-blotch caused by *Selenophoma bromigena* (Sacc.) Sprague and A. G. Johnson. In 1945, moderately severe infection of leaf-blotch in single plant nurseries and solid-seeded plots allowed observations of strain susceptibility. A strain test of northern and southern types sown the previous year was examined and strains scored for resistance to leaf-spot damage. Table 3 presents the average rating of strains included in this trial.

All strains of the southern type were significantly higher in resistance to leaf-blotch than the northern commercial strain. No significant difference could be found between strains within either type in resistance to this disease. Rust damage observed to be severe on brome grass of the southern type in the U.S.S.R. (12), was not observed on either type of brome grass at Saskatoon.

TABLE 3.—RESISTANCE OF BROME GRASS STRAINS TO DAMAGE BY LEAF-BLOTCH (*Selenophoma bromigena*), SASKATOON, 1945. STRAINS RATED FROM 1 (SEVERE DAMAGE) TO 5 (NO DAMAGE)

Strain	Damage score	
Northern Type		
Commercial	3.0	
Parkland	3.2	
Iowa-1158	3.0	
Average		3.1
Southern Type		
Achenbach	4.2	
Lincoln	4.2	
B. in. −9	3.8	
Average		4.1
L.S.D. strains (P = 0.05)	0.8	

FIGURE 3. Test of northern and southern strains of brome grass at Saskatoon in the fall of the first year of growth. Note uniformly good establishment of all strains. *Left plot* (47) northern commercial; *right plot* (46) Neb. 44.

Newell and Keim (10), Anderson (1), and Lambert (9) have indicated that in fall seedings under southern conditions much greater seedling vigour is shown by southern strains. In spring seedings at Saskatoon no difference has been noted in field trials in the vigour of seedlings or uniformity of stands between southern and northern types. In 1948 a six-replicate plot test of southern and northern strains was sown on May 18 and harvested on August 20 to obtain information of the rapidity of establishment. Varieties of the northern type in this test were northern commercial, Parkland, and Martin. Varieties of southern type were Achenbach, Lincoln, Neb. 36, and Neb. 44. Yields of over one ton per acre were obtained but no significant difference was found between strains. Figure 3 gives a general view of this test prior to cutting for hay and indicates the overall good establishment of strains.

Self- and Cross-Fertility

During 1945 and 1946 a total of 95 plants of the northern type and 59 plants of the southern type were observed for self- and open-fertility at Saskatoon. Determinations of self-fertility were made on the basis of seed-setting within three parchment bags while determinations of open-fertility were made on the basis of seed-setting of duplicate samples of 10 open-pollinated panicles. Table 4 shows the distribution of plants according to self- and open-fertility ratings.

It is apparent from Table 4 that there is little difference between northern and southern types in self-fertility or open-fertility as shown either by the average set of seed or the distribution of plants for level of

TABLE 4.—SELF- AND OPEN-FERTILITY RATINGS OF NORTHERN AND SOUTHERN TYPES OF BROME GRASS. PLANTS RATED ACCORDING TO THE NUMBER OF SEEDS FORMED PER PANICLE. SASKATOON, 1945-1946

Type	Percentage of plants with fertility ratings of:									
	0.0	0.1–1.0	1.1–10.0	10.1–20.0	20.1–40.0	40.1–80.0	80.1–120.0	120.1–200.0	No. of plants	Average fertility
Self-fertility										
Northern	3	13	48	18	11	6	1	—	95	10.9
Southern	10	13	46	20	7	2	—	2	59	9.9
Open-fertility										
Northern	—	—	1	2	11	39	32	15	95	77.2
Southern	2	2	2	2	13	35	24	20	59	79.2

seed setting. It is interesting to note that under open-pollination both types produced about an equal number of seeds per panicle. Since the southern type has been shown to be lower in seed production than the northern type, it would appear that this was due to the production of fewer seed culms rather than due to the presence of smaller panicles or sterility in the southern type. The failure to obtain any difference in self-fertility between the two types is in keeping with the results of Zerebina (12), and Lambert (9).

In 1948 the ability of the two types to intercross was studied at Saskatoon by pollinating two plants of the southern type and one of the northern type with pollen from four plants of the southern type and six plants of the northern type. The method of crossing consisted of placing detached panicles of the ten pollen parents within separate pollination bags applied previously to the seed parents. This transference was made just after first flowering had taken place and transferred panicles were kept alive in the new environment by placing the bases of stems in water. Not all combinations were completed due to a failure to obtain complete correspondence in flowering and due to the loss of several combinations from wind damage. Table 5 presents data showing the success of seed setting on the crosses that were harvested.

TABLE 5.—INTERFERTILITY OF NORTHERN AND SOUTHERN TYPES OF BROME GRASS AS SHOWN BY CONTROLLED POLLINATIONS OF SELECTED PLANTS, SASKATOON, 1948

Type of cross	Number of crosses	Average seed-setting in terms of seeds per panicle		
		Controlled crosses	Female parents on	
			Selfing	Open-pollination
Northern × northern	7	62	5	75
Northern × southern	3	38	5	75
Southern × southern	6	69	18	105
Southern × northern	13	66	18	105

While plants used as female parents in these crosses were not completely self-sterile the increase in seed setting following cross-pollination is indicative of a high degree of crossing. Since the success of seed setting following crossing of different types approaches that from crossing similar types it would appear that the two types of brome grass are cross-compatible. This fact is of significance to the plant breeder wishing to combine the favourable characteristics of the two types.

DISCUSSION

Since southern strains of brome grass have been found inferior in seed yields in these studies it appears undesirable to distribute or license the sale of these varieties in Western Canada at the present time. Unless much stronger discrimination against Canadian brome grass seed develops within the United States than at present exists growers in Western Canada are not likely to show interest in the southern type. If southern strains were introduced into the present seed areas with a view to seed production the preservation of strain identity would likely be difficult due to the wide distribution and good adaptation of the northern type. However, the advent of varieties of the southern type with good seed yields might warrant production of these varieties outside the present seed districts. The drier brown soil zone where the southern type has shown some advantage in yields of forage and where the northern type is not widely grown at present might be considered as an area for the production of southern strains.

The greater disease resistance of the southern type is a character making the southern type of interest in the brome grass improvement programme. At the Dominion Experimental Farm at Brandon and the Dominion Forage Crops Laboratory at Saskatoon selection is being carried on within both the northern and southern types for plants with high forage and seed yields and for resistance to leaf-spot diseases. In view of the fact that most of the brome grass seed produced in Western Canada is being sold on markets in the United States and that bred strains from Canada have performed particularly poorly in the United States, it is imperative that new varieties be acceptable in the United States before being distributed in Canada.

Named and numbered strains of the northern type have shown no superiority in forage or seed production over the northern commercial type and this fact may be taken as a reflection on the methods of producing these strains. The Superior variety was developed by the mass selection of a small number of plants of the northern type and differs from the commercial type in being slightly less strongly creeping. The Parkland variety and strains S-23-7 and S-23-12 were developed by repeated selection within inbred lines and are definitely less strongly creeping than the original commercial type. Had tests of combining ability been applied in the production of these strains higher yields of seed and forage might have been obtained. It should be pointed out that these four strains form a negligible part of the Canadian seed trade at the present time. The Parkland variety which showed promise as a less strongly creeping variety is no longer recommended in Saskatchewan in view of its low seed yields. No

investigations have been made of the occurrence of regional strains in Western Canada but general observations of farm fields and experimental plots have indicated no deviation from the general northern type.

The history of the introduction of brome grass to America as presented by Newell and Keim (10), Anderson (1), and Hansen (8) is substantiated by these studies in that two reasonably distinct forms were indicated and correspondence found with similar types in Europe. The southern type which is adapted to the arid steppe regions of the U.S.S.R. was found to be well adapted to the drier zones in Western Canada. The northern type occurring more commonly on alluvial plains and moist meadows in the U.S.S.R. was found to yield somewhat better than the southern type at certain stations within the more moist park belt in Western Canada. Newell and Keim, and Anderson have suggested France and Hungary as sources of the southern strains in America. The occurrence of southern types within the U.S.S.R. as pointed out by Zerebina (12) would suggest that southern types or intermediate forms may have been introduced to America from Russia along with the northern type.

The designation of the two types of brome grass as "southern" and "northern" would infer more marked differences in adaptation and photoperiodic response of the two types than shown in these tests. Southern strains in these tests were fully as hardy as the northern strains and on the average as productive of hay. The marked difference in seed production of the two types might be considered an indication of a differential photoperiodic response but the dates of flowering for the two types differed little. In view of the lower seed yields of southern strains in the second year of production under Nebraska conditions (10) it is probable that southern strains are characteristically low in seed production. A similar response of the two types in Western Canada might be expected in view of the fact that the northern limits of brome grass distribution in Europe lie considerably north of the northern limits of cultivation in America. At latitudes comparable to those of the Canadian stations both northern and southern types occur naturally and are cultivated in the U.S.S.R. Zerebina (12, 13, 14) has indicated that in the Central Chernozem Region of the U.S.S.R. the occurrence of either type is governed by ecological adaptation, particularly adaptation to moisture conditions. From these studies it would appear that a somewhat similar distinction with regard to drought tolerance might be made in Western Canada.

SUMMARY

1. Forage production of southern strains of brome grass at nine stations in Western Canada was found to be similar to that of northern commercial brome grass.

2. Seed production of southern strains at three stations in Western Canada was found to be inferior to that of northern commercial brome grass. The yield of seed of the southern strains Achenbach and Lincoln was about half that of northern commercial brome grass.

3. Northern and southern strains reacted similarly in mixtures with alfalfa as far as total yields were concerned. Tests of mixtures have not been continued for a sufficient period of years to conclude as to the aggressiveness of strains in mixtures.

4. Plants of the southern type showed minor variations in plant type from the northern type particularly with respect to the nature of the leaf and panicle shape.

5. Southern strains were two to four days later in flowering than northern strains and showed more resistance to fall and spring frosts. Southern strains possessed superior resistance to certain leaf spot diseases.

6. The degree of self-fertility and the distribution of plants for level of self-fertility was similar for the two types. In controlled crosses the two types were found to be interfertile.

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ERRATUM

In the article published in the July issue of *Scientific Agriculture*, Volume 29, pp. 345-350, "Prevention of Early Decay of Cut Potato Sets by Chemical Treatment", by G. B. Sanford, an error occurred in the caption for Figure 1. This should read: "Figure 1—A. . . . *fourth row*, uninfested soil, sets not treated; *bottom row*, infested soil, sets not treated."

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